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The effect of age and year on the survival of breeding adult Great Skuas *Catharacta skua* in Shetland

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The survival rates of breeding adult Great Skuas *Catharacta skua* were examined at Foula, the largest colony in the world, where numbers have been declining since the late 1970s. Resightings of colour-ringed breeding adults over a 12-year period were analysed using Cormack-Jolly Seber models to estimate survival rates. Annual survival rates averaged 0.89 but varied among years between 0.82 and 0.93, with annual variations being temporally associated with variations in sandeel abundance during the breeding season. Most birds appeared to die outside the breeding season and so it is possible that nutritional stress and reproductive costs of breeding in years of poor food supply affect survivorship on migration or in the wintering range. Survival rates of adult Great Skuas were affected by their age according to a quadratic equation, with survival increasing significantly with age from 0.73 in 5-year-old-birds to between 0.85 and 0.96 in birds from 7 to 22 years old, with a sharp decline to between 0.75 and 0.87 in birds over 22 years old. Year effects were evident when controlling for age, indicating that annual variations in survival rates are not explained by changes in age-composition of the marked population among years.

Long-term monitoring of the abundance of breeding birds at seabird colonies in Britain have yielded impressive long-term descriptions of their population trends (Cramp *et al.* 1974, Lloyd *et al.* 1991, Thompson *et al.* 1998, Ratcliffe *et al.* 2000). However, the understanding of the stages of the life history that have changed to produce these trends and the proximate or ultimate factors driving them is often poor. Seabird life histories are characterized by high annual adult survival rates, deferred breeding and low reproductive output (Furness & Monaghan 1987) and so their population trends are extremely sensitive to small changes in adult survival rate. Effective diagnosis of the changes driving population trends is therefore dependent on precise and accurate annual survival estimates and an understanding of the extrinsic and intrinsic factors that affect them (Birkhead & Furness 1985, Croxall & Rothery 1991).

Annual variations in seabird survival rates likely to be related to extrinsic environmental influences that are independent of characteristics of the seabird population. Survival rates of adult seabirds are relatively insensitive to annual changes in food availability compared to their breeding success (Cairns 1987, Pons & Migot 1995, Oro *et al.* 1999). However, in some situations, such as those caused by major perturbations in oceanography (Massey *et al.* 1992, Nur & Sydeman 1999), reductions in prey abundance can be so extreme that adult survival is suppressed (Vader *et al.* 1990, Harris & Bailey 1992, Barrett & Krasnov 1996). Other environmental factors that can affect annual survival rates are weather (Spendelow *et al.* 1995, Harris & Wanless 1996) and natural toxins (Potts *et al.* 1980, Coulson & Strowger 1999). Mass mortality events are extreme examples of environmental influences and are a feature of many seabird populations (Potts *et al.* 1980, Harris & Wanless 1996, Coulson & Strowger 1999, Nur & Sydeman

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1999). Such events can be an important aspect of seabird population dynamics and, depending on their frequency and magnitude, may reduce populations to levels below those otherwise imposed by density-dependence (Croxall & Rothery 1991, Nur & Sydeman 1999).

Intrinsic factors that affect survival rates include the size or density of a population and its age-structure. While density-dependent adult survival rates have yet to be demonstrated in seabirds, there is considerable evidence of age-dependence. Young breeding adults may have lower survival rates than experienced ones (Bradley *et al.* 1989, Ainley *et al.* 1990), this being attributed to the death of birds with intrinsically low fitness (Bradley *et al.* 1989). Several studies have documented lower survival rates in very old seabirds (Potts 1969, Pugesek 1987, Rattiste & Lilleleht 1987, Bradley *et al.* 1989, Aebischer & Coulson 1990, Croxall *et al.* 1990, Weimerskirch 1992, Harris *et al.* 1994, Nur & Sydeman 1999) probably resulting from senescence (Newton 1989). Therefore, annual variations in survival rates may be a product of the population's age-structure, especially in populations with unstable age distributions created by variable recruitment or previous mass mortality events.

Great Skuas *Catharacta skua* have a small global population size of approximately 13 600 pairs with a breeding distribution concentrated in north Scotland and Iceland (Lloyd *et al.* 1991). Due to the small population size and restricted range, the Great Skua is classed as a species of conservation concern in Europe (Batten *et al.* 1990). Foula (60°8′N, 2°5′W), a small island (5 km × 4 km) approximately 25 km west of mainland Shetland, supports by far the largest colony of Great Skuas in the world, with around 2500 pairs in the late 1970s and 1980s (Furness 1987), but breeding numbers had declined by 28% of this total by 1992 (Sears *et al.* 1995). An understanding of Great Skua survival rates and the factors that affect them is fundamental to effective diagnosis of the causes of this change in population size. This paper presents estimates of adult survival rates for Great Skuas on Foula based on 12 years of colour-ringing and resighting data and investigates variation in survival rate with year and age. The factors that may be responsible for the annual variations and their role in the population decline are discussed.

METHODS

The study was conducted in the north-east quarter of Foula. Between 1988 and 1996, breeding skuas were trapped on the nest during the incubation period using a clap-net, and were fitted with unique four-ring colour-combinations from which individuals could be identified when subsequently sighted. This resulted in 551 individually colour-marked birds breeding in the study area at least once. Of these, 278 birds were of known age because they had been fitted with monel rings as chicks. Based on studies of other species, colour-ringing is unlikely to affect survival of Great Skuas (Calvo & Furness 1992). The numbers of birds ringed in each year and numbers resighted in subsequent years are given in Appendix 1.

The study area was searched daily for colour-ringed birds by using binoculars and a telescope in all breeding seasons (early May to late July) between 1989 and 1999. Numbers of birds resighted in each year are shown in Appendix 1. Colour-ringed birds were usually resighted at least once every 3 days during the course of studies of their breeding ecology, so resighting probability for birds present within the study area was likely to approach 100%. However, not all Great Skuas returned to breed in the colony every year (Catry *et al.* 1998) and so a small proportion are not present to be resighted. Search effort outside the study area was lower and variable among years and so, to minimize heterogeneity of resighting rates, birds that were colour ringed at nests outside the study area were excluded from analysis.

Great Skuas are extremely faithful to their territories and any movements within the colony are usually very short (Catry & Furness 1997, Catry *et al.* 1997). Indeed, almost all skuas found in consecutive years were on the same territory, so birds were unlikely to be missed because they had moved to another locality. More extensive searches of the whole island were conducted, but no birds that bred in the study area were ever found nesting outside it. There is also no evidence to suggest that colour-ringed Great Skuas that have bred on Foula have moved to other colonies in the Shetland archipelago, despite the fact that several of the colonies are wardened or monitored by other ornithologists and the occurrence of colour-ringed birds would have been noted had they been present. Given the absence of evidence for emigration from the study area, the apparent survival rates presented are likely to be very close to the true survival rates of Great Skuas on Foula.

Ring loss can lead to underestimates of survival rates, and 5.6% of marked birds are known to have lost one or more colour rings during this study.

Degradation of the rings included fading and cracking of the plastic, and some rings slipped inside one another so that only one was visible. Attempts were made to retrap birds with missing rings, but due to skuas being trap-shy for several years after initial capture, the proportion recaptured was relatively small (37%). Those that were recaptured could be identified using the inscription on the monel ring, and had all their colour-rings replaced. Identification of birds missing one or more colour rings that could not be recaptured was possible by a process of deduction using the remaining combination of colour rings, to which leg the monel ring was fitted, and the position of their territory in the colony. In this manner, almost all birds which had lost colour rings were identified with a high level of confidence, and only eight colour-ringed birds of uncertain identity were present at the end of the study.

Cormack–Jolly–Seber models (Cormack 1964, Jolly 1965, Seber 1965) running in the program MARK (White & Burnham 1999) were used to estimate apparent survival rates and resighting probabilities, thus correcting survival estimates for the few birds that defer breeding away from the colony (Catry *et al.* 1998). A model including time dependence in both survival and resighting rates was fitted initially and then Akaike's Information Criteria (AIC) was used to assess the fit of models in which survival and resighting rates were held constant with time (Lebreton *et al.* 1992). Time dependence was retained in the model if its removal resulted in an increase in the AIC of two or more units (Lebreton *et al.* 1992). The significance of time dependence in survival rates was assessed using a likelihood ratio test (Lebreton *et al.* 1992).

The time-dependent CJS models performed on the resighting histories of Great Skuas make specific assumptions about the data (Lebreton *et al.* 1992) and an important first step is to test whether the data fit the model. This was achieved using goodness-of-fit tests running in the program RELEASE (Burnham *et al.* 1987). The data fitted the model with respect to Test 3 ($\chi^2_{16} = 15.57$, $P > 0.4$) but did not fit with respect to Test 2 ($\chi^2_9 = 47.48$, $P < 0.001$), indicating that resighting probability followed a pattern that mimicked trap-dependence (i.e. birds seen in a given year were more likely to be seen the following year than those that were not). This heterogeneity in resighting likelihood was caused by 15 individuals that were alive but absent from the study area for more than one year during the entire study, and was manifested in eight of the 10 years that could be tested. Analyses that included all birds or omitted these 15 individuals (the latter completely removing the trap-dependence effect) were compared to investigate the effect this heterogeneity had on survival and resighting estimates. The differences between the two analyses were small, a similar finding to that for Puffins *Fratercula arctica* on the Isle of May, where a similar trap-dependence problem was corrected by making resighting probability of an individual in year t dependent on whether or not it was seen in year $t - 1$ (Harris *et al.* 1997). Estimates from data including all birds are presented, along with the difference between these estimates and those resulting from data with persistent absentees excluded.

Investigating the effects of age on survival rates from the point when birds were first ringed as chicks could not be conducted using age-specific survival models in MARK. This was because birds ringed as chicks could not be resighted before they were colour-ringed as adults and the age of recapture varied from 5 to 28 years old, thus creating highly heterogeneous resighting rates. The effects of age on survival were instead modelled using logistic regression, with the response variable being whether a bird of a given age in year t survived to year $t + 1$. Birds were included in the analysis only after they had been colour-ringed. 'Back-filling' (Ainley *et al.* 1990) was used to correct survival estimates for those birds spending years away from the colony (i.e. birds seen in year t that were missed in year $t + 1$ but sighted in year $t + 2$ or later were classed being alive in year $t + 1$). The resighting data from 1999 were used solely for back-filling the 1997–1998 survival data. Given the high resighting rates in the latter years of the study and the fact that no birds spent more than one year away from the colony in the late 1990s, the bias due to birds being alive but not resighted in this analysis will be minor.

Non-breeding skuas were trapped by cannon net on club sites (areas where non-breeders gather during the breeding season) and colour-ringed from 1989 to 1993. The 55 known-age birds among them that subsequently recruited into the study population were included in the logistic regression analysis to increase the sample sizes for 5- and 6-year-old-breeders, which are rare owing to the modal recruitment age being 7 years (Ratcliffe *et al.* 1998a). The 17 known-age, colour-ringed birds that recruited into territories outside the study site were excluded from this analysis due to the greater probability of them being missed for more than one year. None of the birds first colour ringed on clubs was included in the Cormack–Jolly–Seber analysis as they would have biased the age structure. The nest-trapped birds should represent a random sample of ages in the study area, whereas recruiting birds will be far younger than the average. Their inclusion in the logistic regression analysis is acceptable as it is age-specific rather than average survival rates that are under scrutiny.

The square of age, as well as age, was included in the logistic regression model to test for quadratic relationships between age and survival rate. Due to small numbers of very old skuas, resightings of birds over 27 years old were pooled. Year was included as a categorical variable to control for annual variability in survival. The interactions of age and year were also modelled to test whether the relationships between survival and age varied among years. A backwards stepwise procedure was used to select the best-fit model.

RESULTS

The overall annual survival rate for Great Skuas between 1988 and 1998 was 0.888 (lower 95% confidence limit (LCL) = 0.875, upper 95% confidence limit (UCL) = 0.899) and the overall resighting probability over this period was 0.956 (LCL = 0.947, UCL = 0.965). Removing time dependence in survival and resighting rates resulted in an increase in the AIC vales of more than 2 (Table 1), indicating that both parameters varied annually. The annual variation in survival among years was significant (G9 = 33.20, $P < 0.0001$), with the pattern being one of decline from 1989 and 1991 before increasing to a plateau between 1994 and 1996 and then being low again in 1997 (Table 2).

Table 1. Models fitted in MARK to determine time dependence of survival rates and resighting probability of colour-ringed Great Skuas in the study site on Foula. The lowest Akaike's Information Criterion (AIC) value is for the model in which both survival and resighting probability are time-dependent, showing this is the best fit model for the data.

Parameter constraint			
Survival rate	Resighting probability	Parameters	AIC value
Time-dependent	Time-dependent	21	2585.05
Time-dependent	Constant	12	2645.68
Constant	Time-dependent	12	2600.10
Constant	Constant	2	2671.39

Table 2. Annual estimates of survival rates (Φ) and resighting probability (*P*) for colour-ringed Great Skuas in the study site on Foula, Shetland. LCL and UCL represent the upper and lower 95% confidence limits of the estimate. Since both survival and resighting rate are time dependent they are confounded in the final year of study and so have been aliased. The 'Difference' column refers to the difference between estimates from the analysis including all birds and that excluding persistent absentees (see Methods).

Parameter	Time period	Estimate	LCL	UCL	Difference
Φ	1988–89	0.864	0.791	0.914	0.015
	1989–90	0.903	0.840	0.943	0.014
	1990–91	0.879	0.810	0.926	0.014
	1991–92	0.824	0.763	0.872	−0.012
	1992–93	0.850	0.794	0.893	0.001
	1993–94	0.867	0.819	0.904	−0.004
	1994–95	0.930	0.892	0.955	−0.009
	1995–96	0.913	0.879	0.939	0.001
	1996–97	0.930	0.896	0.953	0.002
	1997–98	0.840	0.794	0.877	−0.005
	1998–99	–	–	–	
P	1988–89	0.885	0.809	0.933	−0.041
	1989–90	0.888	0.823	0.932	−0.071
	1990–91	0.837	0.765	0.890	−0.059
	1991–92	0.937	0.887	0.966	−0.030
	1992–93	0.934	0.886	0.963	−0.016
	1993–94	0.990	0.963	0.998	−0.005
	1994–95	0.987	0.960	0.996	−0.004
	1995–96	0.983	0.961	0.993	−0.006
	1996–97	0.981	0.955	0.992	−0.008
	1997–98	0.992	0.967	0.998	−0.004
	1998–99	–	–	–	–

Table 3. Likelihood ratio (LR) tests for the significance of the relationship between the specified variables and survival rates of known-age Great Skuas on Foula, Shetland, between 1988–1989 and 1996–1997. The likelihood ratio represents the change in deviance if the given variable is removed from the model with all other variables included.

Variable	LR	*df*	*P*
Age	6.85	1	< 0.01
Age^2	7.54	1	< 0.01
Year	17.05	9	< 0.05
Age*Year	5.61	9	> 0.7

Survival rates of Great Skuas were affected by their age. The model retaining age and its square explained significantly more of the deviance than one with age only (Table 3), indicating a quadratic relationship between age and survival. Survival increased significantly with age, from 0.73 in 5-year-old birds to between 0.85 and 0.96 in birds 7–22 years old, but declined sharply to between 0.75 and 0.87 in birds over 22 years old (Fig. 1). The interactions of age and year were not significant (Table 3),

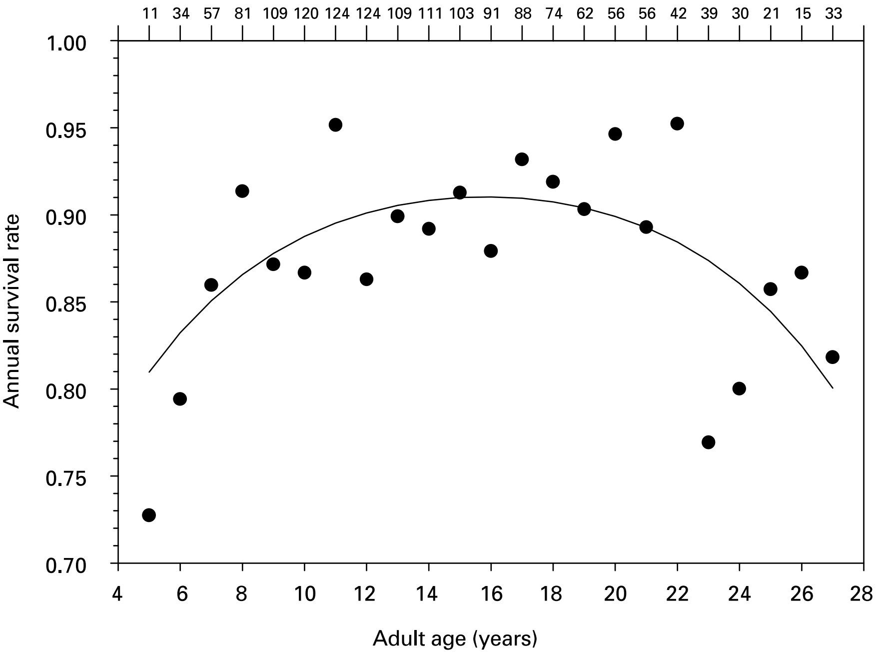

Figure 1. The relationship between age and survival rate of breeding Great Skuas on Foula, Shetland, between 1988–1989 and 1996–1997. Points represent the probabilities of a bird of a given age surviving from year *t* to year *t* + 1. The fitted curve represents the overall effect of age on survival over all years pooled. Numbers along the top of the graph represent the sample size upon which each point is based.

suggesting that the relationship between age and survival was similar among years. The additive effect of year on survival was significant (Table 3) suggesting that the annual variation in survival rates described in the Cormack–Jolly–Seber analysis is best explained by environmental factors rather than changes in the age composition of the marked population among years.

DISCUSSION

This study has resulted in the first maximum likelihood estimates with confidence intervals for Great Skuas, which averaged 0.89 and varied annually between 0.82 and 0.93. Furness (1978) estimated a 0.93 survival rate for Great Skuas between 1938 and 1974 from analysis of ring recoveries which is the same as the highest survival rate observed in this study, although the methods for estimating survival rates in these studies are not the same. Other CMR studies of skuas and large *Larus* gulls have documented survival rates in the order of 0.8 and 0.9 that are similar to those found for Great Skuas in this study, although the overall estimate for Foula Great Skuas is the lowest for any *Catharacta* skua population yet studied, despite the fact that other studies are based on return rates and are likely to be underestimates (Table 4).

Significant variations in survival rates of Great Skuas were identified in this study that could not be explained by variation in the demography of the colour-marked population, suggesting that environmental processes were responsible. Establishing causality between marine processes and seabird population dynamics is notoriously difficult (Harris & Bailey 1992). Few of the colour-marked Great Skuas went missing or were found dead during the breeding season, suggesting that most of the mortality occurs during migration through the North Sea and west coast of Britain, or in the wintering areas, which are mainly around the Iberian coast (Furness 1987, Klomp & Furness 1992a). One of the main known sources of mortality for Great Skuas in Iberian waters is net entanglement, although the importance of this is doubtless over-emphasized by a high reporting rate (Klomp & Furness 1992a). Availability of food is more likely to be an important determinant of survival rates in seabirds during winter, as found for alcids in the North Sea (Harris & Bailey 1992).

However, overwinter survival of seabirds can also vary as a result of stresses occurring in the breeding season (Pugesek 1987, Reid 1987) and survival rates

Table 4. Average survival rates (Φ) estimated from CMR studies for adult breeding skuas and large *Larus* gulls. The method column refers to the approach used in analysis, in which CJS is a Cormack–Jolly–Seber analysis in which resighting rates are modelled and RR is return rates in which resighting rates are assumed to be 100% or 'back-filled' based on subsequent resighting history.

Species	Locality	Φ	Method	Reference
Catharacta skua	Foula	0.89	CJS	This study
Catharacta maccormicki	Antarctica	0.94	RR	Wood (1971)
Catharacta maccormicki	Antarctica	0.96	RR	Ainley *et al.* (1990)
Catharacta lonnbergi	Signy Is.	0.93	RR	Burton (1968)
Catharacta hamiltoni	Gough Is.	0.93	RR	Furness (1987)
Stercorarius parasiticus	Scotland	0.89	RR	Furness (1987)
Stercorarius parasiticus	Foula	0.90	RR	Phillips and Furness (1998)
Larus argentatus	England	0.92	RR	Coulson and Butterfield (1986)
Larus argentatus	France	0.88	CJS	Pons and Migot (1995)
Larus argentatus	Scotland	0.94	RR	Chabrzyk and Coulson (1976)
Larus argentatus	Wales	0.81	CJS	Poole *et al.* (1998)
Larus argentatus	Scotland	0.88	CJS	Wanless *et al.* (1996)
Larus fuscus	Wales	0.90	CJS	Poole *et al.* (1998)
Larus fuscus	Scotland	0.91	CJS	Wanless *et al.* (1996)
Larus occidentalis	USA	0.81	RR	Spear *et al.* (1987)
Larus glaucescens	USA	0.83	RR	Reid (1987)

on Foula appear to be temporally associated with changes in food supply during summer. From 1988 to 1990 the abundance of Sandeels *Ammodytes marinus*, the preferred prey of Great Skuas (Furness & Hislop 1981), was extremely low in Shetland waters (Wright & Bailey 1993). During this period, a higher proportion of experienced Great Skuas on Foula did not attempt to breed (Catry *et al.* 1998) and those that did mostly failed (Hamer *et al.* 1991). This study provides evidence that adult survival rates also underwent a decline during this period, perhaps due to the low availability of food for self-maintenance reducing adult condition and hence survivorship later in the year. This may have been exacerbated by Great Skuas exerting high reproductive effort in an attempt to maintain the growth rates of their chicks (Hamer & Furness 1991, Hamer *et al.* 1991) and this has been shown to reduce the survival rates of gulls (Pugesek 1987, Reid 1987, Pugesek & Deim 1990). Increased adult mortality associated with reduced food supply in seabirds is exceptional (Cairns 1987) but has been documented previously in alcids (Vader *et al.* 1990, Barrett & Krasnov 1996) and Brandt's Cormorants *Phalacrocorax penicillatus* (Nur & Sydeman 1999).

Sandeel abundance increased dramatically in Shetland waters in 1991 (Wright & Bailey 1993). Associated with this was an increase in the proportion of Great Skuas that bred (Catry *et al.* 1998), and an improvement in their reproductive success (Phillips *et al.* 1997, Ratcliffe *et al.* 1998b). During this study, skua survival rates were at their lowest in 1991–1992. They subsequently improved to peak at 0.91–0.93 from 1994 to 1996. Survival rates from 1997 to the following year returned to low levels comparable with those prior to 1994. During 1997, skua chick diets on Foula contained few Sandeels, and breeding success of skuas throughout Shetland was very low (Thompson *et al.* 1997), suggesting low Sandeel availability. Although the temporal coincidence of variations in summer food supply and overwinter survival are compelling, further analyses of skua survival rates and Shetland Sandeel stock estimates over a longer time-series are desirable.

The survival of Great Skuas varied significantly with age, being low in young birds aged less than 7 years and in old birds over 22 years of age. Quadratic age-specific patterns of breeding probability (Catry *et al.* 1998), clutch size (Ratcliffe *et al.* 1998b) and egg volume (Hamer *et al.* 1991) are also exhibited by Great Skuas on Foula. Lower survival rates in young breeders have been documented in South Polar Skuas *Catharacta maccormicki* (Ainley *et al.* 1990), although no declines with old age were detected in their study, while other studies of age-specific seabird survival have found patterns very similar to those described here for Great Skuas, including Mew (Common) Gulls *Larus canus* (Rattiste & Lilleleht 1987), Short-tailed Shearwaters *Puffinus tenuirostris* (Bradley *et al.* 1989), Black-legged Kittiwakes *Rissa tridactyla* (Aebischer & Coulson 1990), Wandering Albatross *Diomedea exulans*

(Weimerskirch 1992) and European Shag *Phalacrocorax aristotelis* (Harris *et al.* 1994).

The lower survival rates of young birds are probably due to the early death of poor quality phenotypes (Bradley *et al.* 1989, Partridge 1989, Aebischer & Coulson 1990). Primiparous Great Skuas that lay one-egg clutches have a significantly lower return rate than those that lay two, suggesting that low fitness in young birds is manifested in both breeding performance and survival rate (Ratcliffe *et al.* 1998a). The decline in survival rates with old age observed in many bird species is generally attributed to the effects of senescence (Newton 1989). The quadratic relationships between breeding probability, clutch size and egg volume observed in Great Skuas on Foula (Hamer *et al.* 1991, Catry *et al.* 1998, Ratcliffe *et al.* 1998b) are likely to be due to similar processes.

Although age affects the survival of individuals, age structure of the population is unlikely to cause large variations in annual survival rates. This is because the age classes for which survival is low are rare (representing 11% of the total breeding population) as few birds recruit below the age of 7 years and few birds survive beyond 22 years. Consequently, little variation in annual survival is likely to be explained by changes in demography. This contrasts with environmental effects that influence the whole population.

Further studies of Great Skua population dynamics are required to estimate prebreeding survival rates reliably. Studies based on live resightings of birds marked as chicks at a single colony are generally confounded by permanent emigration. However, natal philopatry in Great Skuas is very high (Klomp & Furness 1992a), so analyses of birds ringed as chicks and retrapped on club sites may yield reasonably accurate prebreeding survival rates. Analysis of ring-recoveries of dead birds is the most frequently used method of generating independent estimates of prebreeding survival rate for seabirds (e.g. Wernham *et al.* 1997), but since virtually all Great Skuas have been ringed as chicks (Toms & Clark 1998), age-specific recovery and survival rates are confounded (Anderson *et al.* 1985). Recent attempts to model survival rates of Great Skuas from dead recoveries failed to produce reliable prebreeding survival estimates for this reason (S. Freeman [BTO], pers. comm).

The lack of prebreeding survival estimates prevents the prediction of population trends on Foula or complete diagnosis of observed declines. However, the decline in the Great Skua population between the late 1970s and 1992 (Sears *et al.* 1995) is best explained by a reduction in adult survival rate. This is because modal age of first breeding for Great Skuas is 7 years (Ratcliffe *et al.* 1998a), so that effects of breeding failure would not have been manifested until 1995. Survival improved in 1994–1995, but by this time the extremely small 1988, 1989 and 1990 cohorts would have been recruiting (Klomp & Furness 1992b), causing the population to decline for a further 3 years. Since 1997, recruitment from larger cohorts will have started augmenting the breeding population and this may have been adequate to have halted or initiated a reversal of the decline. A complete census of Great Skuas in Scotland was conducted in 2000 and 2001, and analysis of these data will reveal the effects of the perturbation in Sandeel abundance on the Great Skua population at Foula and other colonies in Shetland.

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Appendix 1 Numbers of Great Skuas nest trapped in each year of ringing and numbers seen in each subsequent year. The total is the sum of the number of birds trapped and seen in each year; *n* is the number seen divided by the resighting probabilities given in Table 2 plus the number of newly marked birds released and gives an estimate of the number of colour-ringed birds alive in the sample during each year.

Ringing year	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999
1988	136	104	94	74	62	52	44	36	32	28	23	20
1989		57	46	42	34	30	29	27	25	23	18	13
1990			30	22	23	18	14	14	13	12	11	12
1991				63	57	46	46	44	39	35	30	27
1992					40	35	29	26	21	20	19	18
1993						66	61	60	57	53	44	40
1994							45	41	39	36	34	31
1995								105	94	90	74	69
1996									9	8	6	6
Total	136	161	170	201	216	247	268	353	329	305	259	236
n	136	175	188	228	228	260	270	356	335	311	261	–